

Batesian-Müllerian mimicry ring around the Oriental hornet (*Vespa orientalis*)

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Abstract

Mimicry is usually understood to be an adaptive resemblance between phylogenetically distant groups of species. In this study, we focus on Batesian and Müllerian mimicry, which are often viewed as a continuum rather than distinct phenomena, forming so-called Batesian-Müllerian mimicry rings. Despite potent defence and wide environmental niche of hornets, little attention has been paid to them as potential models in mimicry research. We propose a Batesian-Müllerian mimicry ring of the Oriental hornet (*Vespa orientalis*, Hymenoptera: Vespidae) consisting of eight species that coexist in the Mediterranean region. To reveal general ecological patterns, we reviewed their geographical distribution, phenology, and natural history. In accordance with the ‘model-first’ theory, Batesian mimics of this ring occurred later during a season than the Müllerian mimics. In the case of Batesian mimic *Volucella zonaria* (Diptera: Syrphidae), we presume that temperature-driven range expansion could lead to allopatry with its model, and, potentially, less accurate resemblance to an alternative model, the European hornet (*Vespa crabro*: Hymenoptera: Vespidae). Colour morphs of polymorphic species *Cryptocheilus alternatus* (Hymenoptera: Vespidae), *Delta unguiculatum* (Hymenoptera: Vespidae), *Rhynchium oculatum* (Hymenoptera: Vespidae), and *Scolia erythrocephala* (Hymenoptera: Scoliidae) appear to display distinct geographical distribution patterns, and this is possibly driven by sympatry with alternative models from the European hornet (*Vespa crabro*) complex. General coevolution patterns of models and mimics in heterogenous and temporally dynamic environments are discussed, based on observations of the proposed Oriental hornet mimicry ring.

Keywords

biogeography, Conopidae, Diptera, evolution of mimicry, Hymenoptera, phenology, polymorphism, Syrphidae

Introduction

Mimicry is an example of convergent evolution whereby similar appearances result in an evolutionary advantage, such as reduced risk of predation. Various defences in animals were described; however, most discussed are Batesian (Bates 1863) and Müllerian (Müller 1879) mimicry. Batesian mimicry is an asymmetrical interaction between a model, chemically or otherwise defended, and a palatable mimic (Bates 1863). Müllerian mimicry is a mutualistic interaction between two or more species, where their shared resemblance and defences protect them from predation with the learning costs, caused by naïve predators, spread among them (Müller 1879; Kapan 2001).

Although traditionally viewed as a parasitic interaction, Batesian mimicry could be beneficial to the defended model under certain circumstances, as it could decrease the error costs caused by a forgetful predator; this phenomenon is called quasi-Müllerian mimicry (Speed and Turner 1999). On the other hand, species involved in Müllerian mimicry could be unequally defended (Speed 1993), forming so called quasi-Batesian mimicry, where the least defended species gains more profit from the interaction (Speed 1993; Balogh et al. 2008). In addition, the level of defence could even vary within one species (Tuskes and Brower 1978; Ritland and Brower 1991) and the same defence could be unequally effective against various predators (Hotová Svádová et al. 2010). Therefore, Batesian and Müllerian mimicry are often viewed as a continuum, rather than distinct phenomena forming so called Batesian-Müllerian mimicry rings (Mallet and Gilbert Jr. 1995). However, species are usually assigned to a Batesian or Müllerian group for practical reasons (as in this study), hence the classification into subtle classes is problematic.

In various mimicry complexes we can find Batesian mimics, which resemble their models rather imperfectly (Sherratt 2002; McLean et al. 2019). The existence of imperfect mimicry has puzzled evolutionary ecologists for a long time (Bates 1862; McLean et al. 2019). Many hypotheses have been proposed so far to explain it, such as e. g. relaxed selection in small-bodied species (Penney et al. 2012), trade-off between mimicry and thermoregulation (Taylor et al. 2016b), effect of community diversity (Wilson et al. 2013), or resemblance to more than one model (Sherratt 2002). It might also be possible that the natural predators, such as insectivorous birds, perceive inaccurate mimics as rather perfect (Cuthill and Bennett 1993), as most studies have evaluated mimetic accuracy using human observers (Taylor et al. 2017; Hassall et al. 2019; Kelly et al. 2021) or image analysis (Penney et al. 2012; Taylor et al. 2016a), and only a few studies considered a perception of real predators (Mostler 1935; Dlusski 1984; Dittrich et al. 1993; Hotová Svádová et al. 2010).

The phenology of mimicry complexes can range from models and mimics occurring at the same time (temporal sympatry), models occurring first, or mimics occurring first in a season. Mathematical modelling (Bobisud 1978) and experiments with human observers (Hassall et al. 2019) supported the model-first scenario as the most beneficial for the models and predators, as the avoidance learning of predators is not biased by encountering a palatable prey of similar appearance. Moreover, it was observed in butterflies (Rothschild 1963), salamanders (Brodie 1981), and might be common among hoverflies (Howarth and Edmunds 2000; Hassall et al. 2019). Some hoverfly species occur earlier than their models (Waldbauer 1988; Howarth and Edmunds 2000; Hassall et al. 2019); however, such scenario is not necessarily harmful to a mimic's fitness, as during spring, the naïve fledglings are still fed by their parents, and the adult birds probably remember the aposematic colouration from the previous season (Waldbauer 1988). Some differences in phenological patterns probably stem from various ecology of the mimics (e.g. larval strategy, preferred habitat, community diversity, mimetic accuracy).

Mimics face increased predation when they occur outside the geographic range of their models (Pfennig et al. 2001), quite often limited by latitudinal gradient (Hines and Williams 2012) or biotope preferences (Wilston et al. 2012). Moreover, the distribution of models may limit the distribution of mimics (Ries and Mullen 2008). However, allopatry between mimics and models, especially at the edge of their distribution range, might be more common than previously thought (Pfennig and Mullen 2010). On the other hand, allopatry is sometimes rather illusory, as mimics could resemble different models in various parts of their distribution area (reviewed in Ruxton et al. 2019).

Here, we focus on the Batesian-Müllerian mimicry ring around the Oriental hornet (*Vespa orientalis*), a large and conspicuous social wasp occurring in Mediterranean, Southwest Asia, Central Asia and Northeast Africa. We identified seven species from various families of hymenopterans and dipterans that are likely Müllerian and Batesian mimics of *Vespa orientalis*. In the present paper, the information on ecology and biogeography of the *Vespa orientalis* mimicry ring are summarised and the following questions are addressed: 1) Which phenological pattern applies to the proposed mimicry ring (model first; mimic first; temporal sympatry)? 2) Are the mimics of the Oriental hornet (*Vespa orientalis*) sympatric with their model across their whole distribution area? 3) Is there spatial overlap between the mimicry rings of the Oriental hornet (*Vespa orientalis*) and the European hornet (*Vespa crabro*)?

Materials and methods

We observed the mimicry ring around the *Vespa orientalis* on the Aegean island of Lesbos (Greece), from 27. viii. to 17. ix. 2019. We explored various habitats (chestnut forest, steppes, salt marshes, macchia) on the island (Fig. 1) and collected specimens of seven (out of eight) species studied, see Table 1. All specimens were collected using

entomological net by Antonín Hlaváček and Jiří Hadrava and are deposited in their private collections. Letters in Fig. 1 refer to localities. Specimens were photographed with a Canon EOS 70 D camera equipped with a Canon EF-S 60 mm f/2.8 Macro USM lens. Zerene Stacker was used for photo stacking (P-max algorithm).

We searched for species with similar colouration pattern occurring in the Mediterranean area. Based on these criteria, we included *Scolia erythrocephala* F. 1775. However, we presume that the *Vespa orientalis* mimicry ring is probably much larger in the eastern (Asian) part of its distribution and might include species such as *Delta pyriforme* (F. 1775), *Laphria dizonias* Loew, 1864, *Monoceromyia eumenioides* (Saunders, 1842), *Rhodanthidium superbum* (Radoszkowski, 1876), *Scolia flaviceps* Eversmann, 1846 (present in Asia Minor, with some records from Greece and Turkey), or *Stiphrolamyra pleskei* (Becker, 1913). Nevertheless, those species were omitted due to the lack of data and will be explored in further studies.

We classified the species into Müllerian and Batesian mimicry groups. The Müllerian group was represented by five species of hymenopterans (*Cryptocheilus alternatus*, *Delta unguiculatum*, *Scolia erythrocephala*, *Vespa orientalis*, and *Rhynchium oculatum*). The Batesian group was represented by three species of dipterans (*Conops flavicaudus*, *Milesia crabroniformis*, and *Volucella zonaria*).

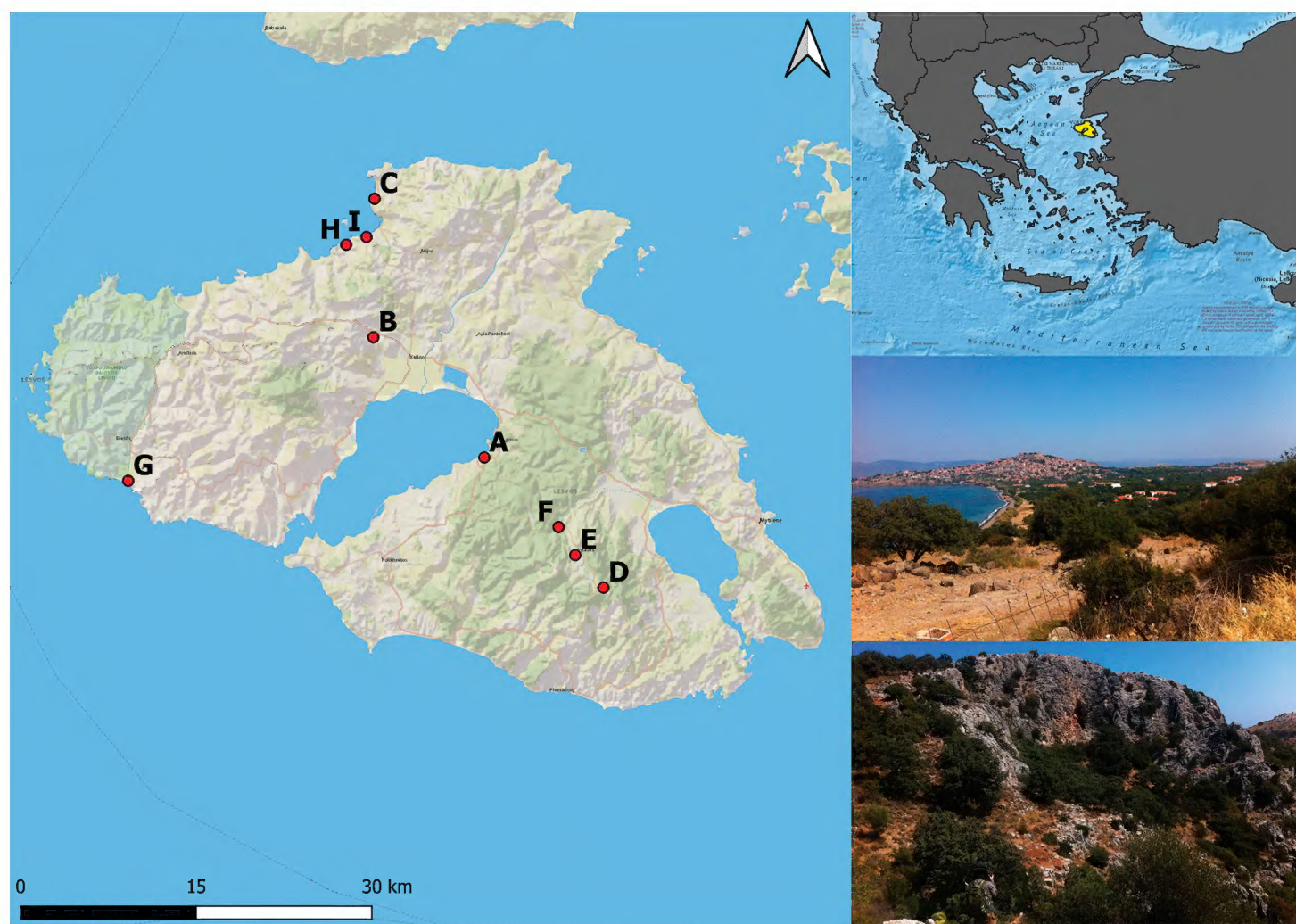


Figure 1. Lesvos Island and collecting sites. From top: map of the Aegean Sea with Lesvos island highlighted; shrubland near the town of Petra, and shrubland in the western part of the island, typical habitat of species from *Vespa orientalis* complex. Letters refer to localities listed in the species list.

Table 1. Species from *Vespa orientalis* mimicry ring observed on Lesvos. Letters refer to localities, displayed in Fig. 1.

| Species | Collecting sites, date and recorded specimens |
|----------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| <i>Vespa orientalis</i> L. 1771 | A: Achladeri, 39°9.42277'N, 26°17.04810'E, 29.8.2019, 1♀, C: Molivos, 39°21.09045'N, 26°10.42042'E, 2.9.2019, 1 ♂. Widely distributed and abundant species throughout the island. |
| <i>Rhynchium oculatum</i> (F. 1781) | C: Molivos, Petrified forest, 39°21.09045'N, 26°10.42042'E, 2.9.2019, 1 ♂, H: Anaxos Skoutarou, 39°18.98855'N, 26°8.74678'E, 2.9.2019, 1 ♂ and 1♀, I: Petra, 39°19.34400'N, 26°9.94130'E, 2.9.2019, 2 ♂, G: Skala Eresou, 39°8.20328'N, 25°55.88838'E, 12.9.2019, 1♀, E: Agiasos, 39°4.82558'N, 26°22.11272'E, 13.9.2019. 1 ♂ |
| <i>Cryptocheilus alternatus</i> (Lepeletier, 1845) | B: Kalloni, Moni Leimonos, 39°14.76615'N, 26°10.34943'E, 30.8.2019, 1♀, C: Molivos, 39°21.09045'N, 26°10.42042'E, 2.9.2019, 1♀. Collected on <i>Foeniculum vulgare</i> Mill. |
| <i>Delta unguiculatum</i> (Villers, 1789) | C: Molivos, Petrified forest, 39°21.09045'N, 26°10.42042'E, 2.9.2019, 1 ♂. Collected on <i>Foeniculum vulgare</i> Mill., near a road. |
| <i>Conops flavicaudus</i> (Bigot, 1880) | A: Achladeri, 39°9.42278'N, 26°17.04810'E, 29.8.2019, 1 ♂, A: Achladeri, 39°9.27038'N, 26°16.88825'E, 29.8.2019, 1♀ Collected on shrubs in an olive orchard near the coast. Several specimens were observed at this spot, but nowhere else on the island. |
| <i>Volucella zonaria</i> (Poda, 1761) | E: Agiasos, 39°4.82558'N, 26°22.11272'E, 4.9.2019, 1♀, E: Agiasos, 39°4.82558'N, 26°22.11272'E, 13.9.2019, 2♀. Collected on <i>Hedera helix</i> L., suburbs, apple orchard. |
| <i>Milesia crabroniformis</i> (F. 1775) | D: Agiasos. 39°3.31245'N, 26°23.91593'E, 5.9.2019, 1 ♀, E: Agiasos, 39°4.79915'N, 26°22.25362'E, 6.9.2019, 2 ♂ and 1 ♀, F: Agiasos, 39°6.08465'N, 26°21.27432'E, 15.9.2019, 1♀. Collected on <i>Hedera helix</i> L., suburbs, orchard. |

Information on the distribution, phenology, and habitat preferences were adopted from Syrph the Net databases for hoverflies (Speight 2016), from single faunistic records and studies for hymenopterans (Maidl 1922; Betrem 1935; Giordani Soika 1939; Carpenter and Kojima 1997; Archer 1998a, 1998b; Osten 2000; Tüzün et al. 2000; Ćetković 2002; Osten 2002; Tezcan 2005; Józán 2009; Schedl 2010; Özbek and Anlaş 2011; De Groot 2012; Yildirim 2012; Samin et al. 2014; Yildirim and Lelej 2016; Zachi et al. 2021), and Conopidae (Stuke et al. 2008; Zalat et al. 2009; Stuke et al. 2012). Furthermore, data from open diversity databases such as Fauna Europaea (de Jong et al. 2014), GBIF (2021), and iNaturalist (2021) were incorporated. Distribution ranges were assessed as presence or absence within each country. Records with uncertain taxonomical status were omitted.

We compared the *Vespa orientalis* and its Batesian mimic *Volucella zonaria* to the mimetic pair of two related species, the European hornet (*Vespa crabro*) and its mimic *Volucella inanis* (L. 1758).

Other potential mimics of the European hornet (e.g. *Asilus crabroniformis* L. 1758, *Cimbex connatus* (Schrank 1776), queens of *Dolichovespula media* (Retzius 1783), or *Volucella elegans* Loew, 1862) are neither displayed nor analysed, as it lies beyond the scope of this paper.

Similarity of geographic distribution (counted as presence/absence within the country) was calculated for every model-mimic pair using Lennon’s index of similarity (Lennon et al. 2001). Lennon’s index was chosen in order to avoid the bias caused by intraspecific variability in total area size. The UPGMA clustering method was used to

create a dendrogram based on the distribution of species. Phenological shifts between models and mimics were tested with Mann-Whitney U test (Mann and Whitney 1947), comparing the earliest recorded occurrence within a whole distribution area. Software R version 3.3.3 was used for all statistical analysis (R Core team 2021). Maps were created using QGIS software (2021).

Results

We reviewed the Batesian-Müllerian mimicry ring of eight species from various taxonomical and ecological groups: five species of hymenopterans in three families (Vespidae, Pompilidae, Scoliidae) forming the Müllerian part of the mimicry ring, and three Batesian mimics in two dipteran families (Conopidae, Syrphidae). Photographs, distribution maps, phenological charts and habitat preferences, compiled from previously published data, are presented in Fig. 3. Species accounts have been collated from the literature and can be found in Suppl. material 1: Appendix 1.

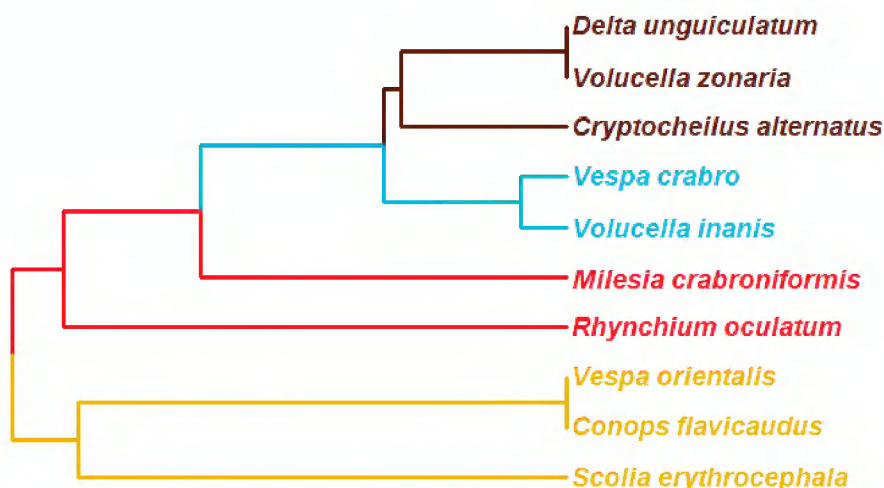


Figure 2. Dendrogram showing similarity between species areas. Lennon's index was used to calculate similarities, the dendrogram was created using UPGMA clustering. Yellow branch: species of Eastern Mediterranean, extending in Levant. Red branch: species present in the entire Ponto-Mediterranean area. Brown branch: Species that extended their range and are present even in central and northern Europe. Blue branch: *Vespa crabro* mimicry ring with *Volucella inanis*.

The phenology of all species overlaps to some degree. Batesian mimics occur later (median of first occurrence: 7, mean of first occurrence: 6.75; counted in months) than their models (median of first occurrence: 3.5, mean of first occurrence: 4.17) corresponding with the 'model first scenario' (p-value = 0.04, Mann-Whitney test).

The distribution of species was reviewed (Fig. 2). The *Vespa orientalis* ring occurs in the Ponto-Mediterranean area, where some species more or less extend the Mediterranean area and occur in central Europe or in the Middle East. The data presented in Fig. 2 suggests that species form 4 different branches: I) Species of Eastern Mediterranean, extending in Levant – *Conops flavicaudus*, *Scolia erythrocephala* and *Vespa orientalis* (yellow branch in Fig. 2); II) Species present in the entire Ponto-Mediterranean area








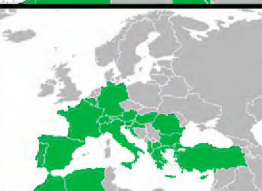












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Figure 3. Members of *Vespa orientalis* and *Vespa crabro* mimicry rings: distribution maps, phenological charts, and preferred habitat. Phenology is simplified to a monthly scale, hab. - habitat. Photos were taken by the authors.

– *Milesia crabroniformis*, *Rhynchium oculatum* (red branch in Fig. 2), III) Species that extend their range and are present even in central and Northern Europe – *Cryptocheilus alternatus*, *Delta unguiculatum*, *Volucella zonaria* (brown branch in Fig. 2), which is therefore close to IV) *Vespa crabro* and its mimic *Volucella inanis* (blue branch in Fig. 2).

Discussion

In the Oriental hornet mimicry ring, the Batesian mimics were found to occur later in the season than the Müllerian mimics. All species overlapped in the late summer. These results are consistent with the ‘model-first’ scenario (Bobisud 1978), which seems to be the most advantageous scenario for the models (Hassall et al. 2019) and is common among hoverflies (Howarth and Edmunds 2000; Hassall et al. 2019). On the other hand, for the Batesian mimics, temporal sympatry with their models would be more beneficial than model-first scenario (Hassall et al. 2019). However, two of the Batesian mimics, *Volucella zonaria* and *Conops flavicaudus*, develop as commensals/parasites in the nests of social hymenopterans, which likely prevents them from activating earlier than the models; *Volucella zonaria* is commensal in ground nests of yellow-jacket wasps (*Vespula germanica*) (Morris and Ball 2004). *Conops flavicaudus* probably develops as a parasitoid of some hymenopterans, such as bumblebees, even though its larval ecology is unknown. This is in line with the previous results, that the constraints set by larval strategy might play a significant role in phenological patterns in some hoverflies (Howarth and Edmunds 2000).

Based on the analysis of geographic distribution, we assigned the species into three groups (‘branches’): Eastern Mediterranean branch (yellow in Fig. 2); Mediterranean branch (red in Fig. 2); and extending Mediterranean branch (brown in Fig. 2), which extends to the Central and/or Northern Europe. However, the distribution areas of the branches are partially overlapping; thus, some species are present in the area defined by the other branches. The Eastern Mediterranean branch is represented by *Vespa orientalis*, the rare Batesian mimic *Conops flavicaudus*, and Müllerian mimic *Scolia erythrocephala*, where all of them are also found in the Levant and in the Middle East. The Eastern Mediterranean could be considered as the centre of the mimicry ring as all species are present in Greece and Turkey (the geographic distribution might be incomplete due to missing observational data). The Mediterranean branch consists of species common in the whole Mediterranean area, i.e. Batesian mimic *Milesia crabroniformis* and Müllerian mimic *Rhynchium oculatum*. Three species (Batesian mimic *Volucella zonaria*, and Müllerian mimics *Cryptocheilus alternatus* and *Delta unguiculatum*) of the described mimicry ring are present in the whole Mediterranean area, and moreover, they extend their range into Central Europe or, in the case of *Volucella zonaria*, even into Northern Europe (Morris and Ball 2004), thus forming ‘extending Mediterranean’ branch, which partially overlaps with the distribution of the European hornet (*Vespa crabro*) and its mimicry ring.

We consider *Vespa orientalis* to be the ‘leading model’ of the studied mimicry ring.

Vespa orientalis is, in contrast with other Müllerian mimics in complex, habitat generalist, making it an ideal ‘leading model’. Unlike the other Müllerian mimics of the mimicry ring, *Vespa orientalis* is a social species, living in colonies which could number thousands of workers (Ishay 1976); therefore, it could occur in higher numbers than solitary hymenopterans. Moreover, the lethal capacity of venom is known to positively correlate with the degree of sociality in aculeate hymenopterans (Schmidt 2014), which might implicate that social hymenopterans possess generally more potent venom than their solitary relatives. However, *Vespa orientalis* is completely missing in the Western Mediterranean (yet some observations from past years were made by Hernández et al. 2013). That leads to the question, which species is the ‘leading model’ for Batesian mimics in this part of Europe. We propose the following: a) *Vespa crabro*, b) either *Cryptocheilus alternatus*, *Delta unguiculatum* or *Rhynchium oculatum*, c) combination of several of the listed species play the role together, and d) there is no ‘leading model’ outside the range of *Vespa orientalis*. Based on high noxiousness and sociality, we could hypothesize that *Vespa crabro* might be an important model in the Western Mediterranean. More observational data and experimental evidence would be needed to resolve the relationships between the Müllerian part of the mimicry ring.

Colour polymorphism was described in some members of the mimicry ring. Interestingly, black morphs occurred sympatrically with the European hornet (*Vespa crabro*). Specifically, Batesian mimic *Volucella zonaria* sometimes tends to be darker with a black, ‘*Vespa crabro*-like’ pattern on the thoracic dorsum in some locations, i.e. in Corsica (van der Goot 1961), or the Czech Republic (personal observation). Dark colouration of the thorax and petiole was also observed in German populations of Müllerian mimic *Delta unguiculatum* (Mader 2000). Dark morphs of *Cryptocheilus alternatus* occur on the Iberian Peninsula (personal observation). *Vespa crabro* occurs in the mentioned locations (Germany, Czech Republic, Corsica, Iberia), whereas *Vespa orientalis* does not. Even higher variability in colouration occurs in Müllerian mimic *Scolia erythrocephala*, where the colouration varies both between and within subspecies from yellow-and-black to ‘*Vespa orientalis*-like’ colouration. Moreover, it was argued that *Scolia* develops darker colouration when it is exposed to lower temperatures during development (Osten 2000). However, the taxonomical status of the *S. erythrocephala* subspecies and its whole species group (*erythrocephala-flaviceps*) is complicated and unresolved; thus, more work would be needed to reveal its geographical colouration patterns.

An interesting case of colour polymorphism occurs in the Müllerian mimic *Rhynchium oculatum*. Three subspecies (sometimes considered as colour forms) of *Rhynchium oculatum* with slightly different colour pattern have been described (Gusenleitner 2000). In the Eastern Mediterranean, we found *Rhynchium o. hebraeum* (Giordani Soika 1952), with a red thorax and yellow and red patterns on the abdomen, which occurs in sympatry with *Vespa orientalis*, which it closely resembles. In the Central Mediterranean, *Rhynchium o. oculatum* (F. 1781) is present; thus, it overlaps with *Vespa orientalis* as well as with *Vespa crabro*. Interestingly, co-occurrence with both hornet species may

have led to the evolution of a black pattern on the thoracic dorsum and black markings on the yellow abdomen in *Rhynchium o. oculatum*; therefore, it resembles *Vespa crabro* rather than *Vespa orientalis*. In contrast, *Rhynchium o. ibericum* Giordani Soika, 1966, which occurs on the Iberian Peninsula, where only *Vespa crabro* occurs, is mostly red, with a black pattern on the thorax and only small yellow markings on the 2nd tergite. The thorax is darker with less pronounced abdominal patterns, which means it resembles *Vespa crabro* rather imperfectly. Colour polymorphism is affected by abiotic factors such as temperature, documented in various mimics and models (e.g. Dušek and Láška 1974; Osten 2000; Knapp and Nedvěd 2013); thus, the shared black pattern might also be caused by convergent adaptation to the local climate conditions.

Batesian mimic *Volucella zonaria* displays variable mimetic accuracy based on geographic location. We compared the *Vespa orientalis* and its Batesian mimic, hoverfly *Volucella zonaria*, with the related mimetic pair of the *Vespa crabro* and its mimic *Volucella inanis*. Although distribution areas of both mimetic pairs overlap, the area of *Volucella inanis* and *Vespa crabro* is shifted more northwards. However, *Volucella zonaria* undergoes annual migration to Central and Northern Europe and it is expanding northward in recent years (Morris and Ball 2004), resulting in increasing geographical overlap with *Vespa crabro* and *Volucella inanis*, out of the range of *Vespa orientalis*. Thus, in the Mediterranean, *Volucella zonaria* might be a perfect mimic of *Vespa orientalis*, whereas in Northern Europe, it might be an imperfect mimic of *Vespa crabro*. However, as the colouration of this species seems to vary in some localities (van der Goot 1961), more evidence would be needed to confirm this assumption. Interestingly, perfect Batesian mimic *Volucella inanis* occurs in sympatry with its model *Vespa crabro* across its whole geographical range, although it also partly overlaps with *Vespa orientalis*.

In the last few decades a shift of geographic range has been observed in mimics (*Volucella zonaria* in Morris and Ball 2004) as well as models (*Vespa orientalis* in Zachi and Ruicănescu 2021). The rapidly changing climate of Anthropocene could give us a unique opportunity to observe interactions between mimics and their predators, where Batesian mimics are expanding their range beyond that of their models, with a possibility of then developing imperfect mimicry. In addition, climate could also affect the phenological patterns of mimics and their models, leading to more ‘model-first’ interactions (Hassall et al. 2019).

We characterized the Batesian-Müllerian mimicry ring of seven species around *Vespa orientalis* in the western Palearctic. Phenology, natural history, and the distribution of all species were reviewed. Previous studies on phenological patterns of mimics have provided ambivalent results; this study provides evidence that the *Vespa orientalis* mimicry ring fits the ‘model-first’ scenario. Review of distribution revealed differences in areas of species, forming Eastern Mediterranean, Mediterranean, and extending Mediterranean branches. We conclude that colour polymorphic species might resemble two different models (*Vespa orientalis*, *Vespa crabro*) across their distribution range. Moreover, we proposed that mimetic accuracy might vary across the distribution range of the migratory and expanding Batesian mimic *Volucella zonaria*, which seems to be a perfect mimic of *Vespa orientalis*, although an imperfect mimic of *Vespa crabro*.

Conclusion

Our results highlight the complexity of the proposed Batesian-Müllerian mimicry ring around the Oriental hornet (*Vespa orientalis*). Bringing the information on phenology, ecological strategy, colouration patterns and geographical distribution together is an approach that could deepen our understanding of the ecology and evolution of mimicry. We encourage the application of the eco-evolutionary approach to mimicry research, as it could help in further investigations of mimicry rings and explanation of phenomena such as the existence of imperfect mimicry.

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Supplementary material I

Data of distribution

Authors: Antonín Hlaváček, Klára Daňková, Daniel Benda, Petr Bogusch, Jiří Hadrava

Data type: excel file

Explanation note: Distribution data excerpted from literature.

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Link: <https://doi.org/10.3897/jhr.92.81380.suppl1>

Supplementary material 2

Appendix 1

Authors: Antonín Hlaváček, Klára Daňková, Daniel Benda, Petr Bogusch, Jiří Hadrava

Data type: Species account (docx. file)

Explanation note: Natural history of species within *Vespa orientalis* mimicry ring.

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